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NATIVE BEES (HYMENOPTERA: APOIDEA) IN NATIVE TREES: *NYSSA SYLVATICA* MARSH. (CORNACEAE)

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Abstract.—*Nyssa sylvatica* (black gum, sour gum, pepperidge) is a functionally dioecious, insect-pollinated, ornamental, native tree that blooms from late May through early June in eastern Maryland. Its small, green flowers were visited for their abundant nectar and pollen by 46 species of native bees in 13 genera, and by other insects. Although honey bees were locally numerous, few (only 1.5% of all sampled bees), visited *N. sylvatica* and there was no evidence that they displaced native bees on this host. The inconspicuous flowers with vestigial green petals and sepals may attract pollinators by means of the lenslike, spherical droplets of nectar on glaucous floral discs that sparkle in the sunlight, and concentrate and reflect visible and ultraviolet light. Such flowers are here named "sparkle-flowers" (new coinage).

Key Words: *Nyssa,* Cornaceae, gum, tupelo, *Euphorbia, Hedera,* insect pollination, bees, competition, reflective nectar, ultraviolet, "sparkle-flowers"

The original vegetation of eastern North America after glaciation and before agriculture consisted of boreal, temperate and subtropical forests. The many native bee species of this region thus would be expected to be best adapted to forage primarily on native flowering forbs in spring before the forest canopy closes, and on the flowers of native trees and bushes. Our exotic agricultural crops, most ornamental plants, most weeds, and other plants that grow where the primeval forests have been cleared are visited by polylectic native bees, but these are not their original hosts. Surprisingly little is known about the bees and other insects that visit the flowers of our native North American trees, attention being diverted to the remote rainforests of Latin America. In order to learn about the normal relationships of native bees and their hosts, I observed and collected the insects visiting flowers of several species of native trees. Host trees surveyed included red maple, *Acer rubrum* L. (Batra 1985); Allegheny chinkapin, *Castanea pumila* (L.) Mill.; flowering dogwood, *Cornus florida* L.; sassafras, *Sassafras albidum* (Nutt.) Nees (Batra, unpublished), and black gum, *Nyssa sylvatica* Marsh. (this publication). The results of this basic research are expected to be useful for application in natural resource conservation, horticulture, plant breeding, wildlife management, and forestry.

The possible competition with native bees for floral resources by introduced European honey bees has recently become a controversial issue among conservationists (reviewed by Paton 1996). Therefore, *N. sylvatica* trees near a large apiary were included in the survey, to try to find out if honey bees had depleted nectar and pollen, and had displaced native bees.

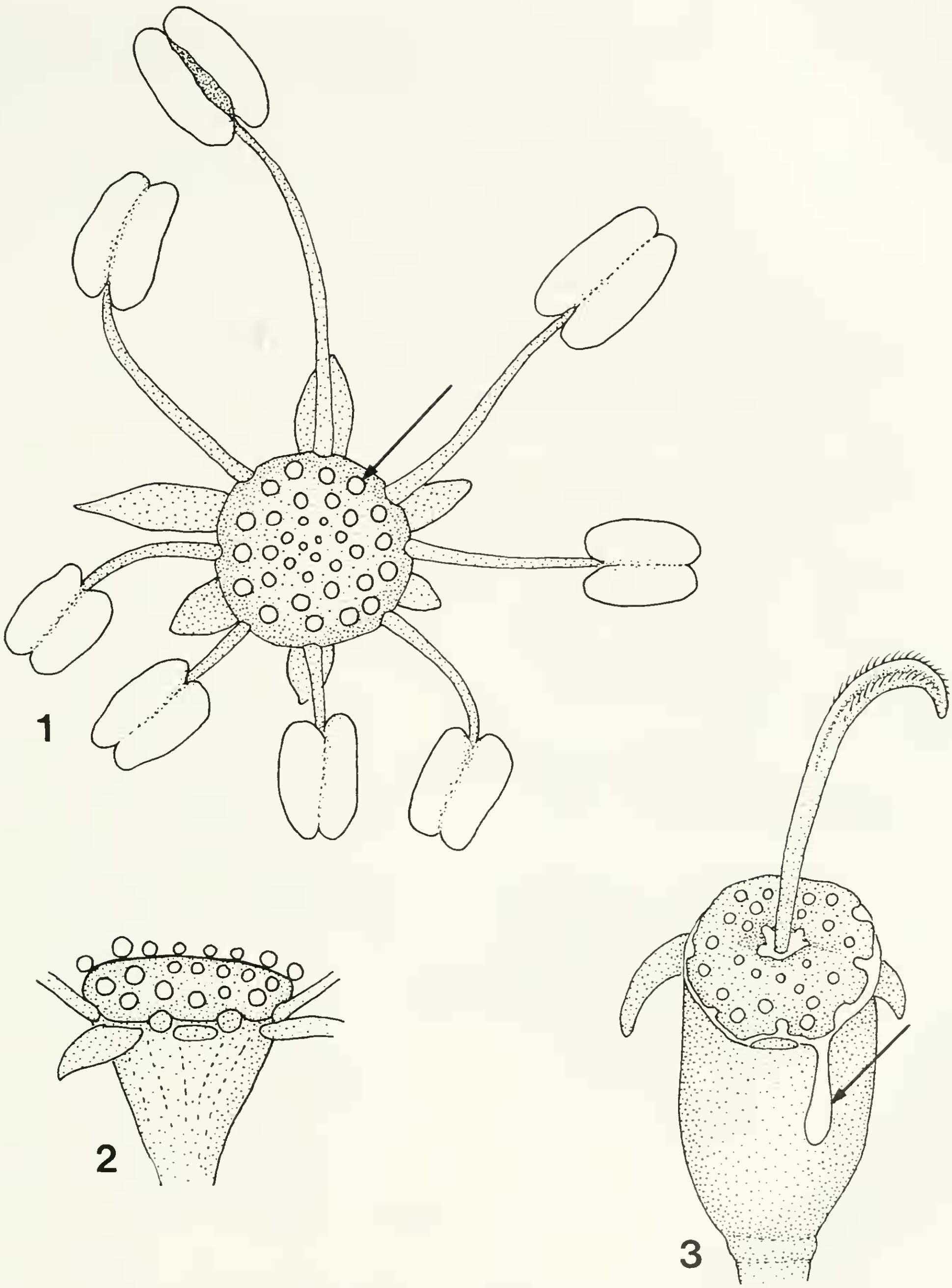
Nyssa sylvatica is an abundant native tree in the mesophytic forests of eastern North America. It ranges from southern Maine through southern Florida, and west through eastern Texas and Michigan, with a small population in the Mexican highlands (Eyde 1963, 1966). Popularly named black gum, black tupelo, sour gum, and pepperidge, it is cultivated as an ornamental tree because of the brilliant red and orange autumnal colors of its glossy leaves, and its attractively drooping, crooked branches. Birds eat its juicy, ovoid blue-black fruit (single-seeded drupes), disseminating this tree. The wood is used for veneer, containers, crossties and pallets.

There are seven species of *Nyssa* worldwide, five of them native to eastern North America, one in eastern China, and one in southeast Asia (Tandon and Herr 1971, Wen and Stuessy 1993). *Nyssa* is closely related to *Cornus,* and it has been included in the Nyssaceae (Eyde 1963, 1966; Tandon and Herr 1971; Cipollini and Stiles 1991) or the Cornaceae (Cronquist 1988). The tupelo, water gum, or white gum, (*N. aquatica* L.), grows in the swamps of the southeastern United States (Eyde 1963). Tupelo nectar is the source of a delicately flavored, expensive honey, which contains 48% levulose and 24% dextrose, and does not granulate; hives of honey bees are taken on barges into the swamps when tupelo blooms (Wood 1958, Rahmlow 1960a,b).

Staminate (male) and pistillate (female) flowers of *N. sylvatica* are borne on different trees; thus, this species is dioecious (Cipollini and Stiles 1991). A few pistillate flowers may have anthers with abortive pollen (Eyde 1963). Male trees bear more numerous and heavier flowers than do female trees. The depletion of nutrients caused by fruiting results in less frequent and less reliable flowering in female than in male trees (Cipollini and Stiles 1991). Flowers appear in the late spring, when the leaves are almost fully expanded. They grow on 3 to 6 cm long pedicels, often below the foliage and largely shaded by leaves. The small (ca. 8 mm long), green, inconspicuous pistillate flowers grow in groups of 2 to 4 on each pedicel. Clusters of staminate flowers are much more conspicuous, due to their larger size, their radiating yellow anthers on long filaments, and the glabrous discs of individual flowers. Several of the small, green staminate flowers (each 3 to 5 mm in diameter) grow on each pedicel, forming spheroid, umbel-like clusters of short racemes, up to 1.5 cm in diameter. Flowers of *N. sylvatica* would appear to be usually pollinated by the wind, due to their small size, green color, faint to no odor, and inconspicuousness. However, Eyde (1963) mentioned unspecified bees and other insects visiting them, also wind-borne pollen, collected 160 m from a tree. Three species of solitary bees, *Andrena hippotes* Robertson, *Perdita bradleyi* Viereck, and *P. townesi* Timberlake have been collected from flowers of *N. sylvatica* (Hurd 1979).

Flowering of *N. Sylvatica*

About twenty trees were studied from May 19 through June 9, 1997. They grew as scattered trees at the edge of a predominantly oak forest near the Bee Research Laboratory at Beltsville, MD, and in a suburban setting near my house in Greenbelt, MD, 4.8 km to the south. Insect visitors in the canopy were observed with the aid of 7 × 50 binoculars, and specimens on flowers were collected with a long-handled, aerial net. The weather was variable, being warm (to 36°C), dry, and sunny from May 19 through 23; cool and rainy from May 24 through 27; then mild and sunny from May 28 through June 9. Rain washed the exposed nectar from floral discs, but it was replenished during dry weather. Flowering began on May 22, when some anthers on the staminate flowers of male trees growing in sunny areas began to dehisce, and small, spherical droplets of nectar were simultaneously secreted (Figs. 1,2). Pistillate trees in sunny areas began to bloom on May 23, also secreting nectar, which accumulated at the bases of their erect green styles and in the grooves surrounding their floral discs



Figs. 1–3. "Sparkle-flowers" of *N. sylvatica*; the cushionlike floral discs are about 2 mm in diameter. 1, Young staminate flower with vestigial green petals, viewed from above; one stamen has elongated and its yellow anther has dehisced; the glaucous floral disc bears reflective droplets of nectar (arrow). 2, Lateral view of the disc of a staminate flower, showing how the spherical, lenslike droplets stand above its surface. 3, Young pistillate flower (oblique view), with droplets of nectar; some droplets have coalesced around the base of the style, and nectar oozes from the floral disc onto the ovary (arrow).

Table 1. Bees caught and seen on flowers of *N. sylvatica*. F = female or worker bee; M = male bee; P = bee is collecting pollen; G = at Greenbelt; B = at Beltsville. Some of the unidentified male and female *Andrena* may be of the same species (the sexes are dissimilar; there are many species of *Andrena*, and many are difficult to identify). The female *Andrena melanochroa* on pistillate flowers was carrying 50% *N. sylvatica* pollen in her well-filled scopae, this shows that bees can pollinate this tree and they will carry pollen a considerable distance (the nearest male tree was over 100 m away).

Bee species or genus, sex and number of individuals		On Male Trees	On Female Trees
Apidae			
2F	*Apis mellifera* L.	—	B
1F	*Bombus bimaculatus* Cresson	P, G	—
1F	*Bombus impatiens* Cresson	P, G	—
Anthophoridae			
1F, 1M	*Ceratina calcarata* Robertson	G	—
5F	*Nomada denticulata* Robertson	G, B	—
1F, 1M	*Xylocopa virginica* (L.)	G	
Megachilidae			
1F	*Chelostoma philadelphi* Robertson	—	G
2M	*Chelostoma philadelphi* Robertson	B	—
Halictidae			
5F	*Augocholora pura* (Say)	2 P, G, B	—
1F	*Dialictus cressoni* (Robertson)	B	—
1F	*D. rohweri* (Ellis)	G	—
1F	*D. tegularis* (Robertson)	B	—
2F	*D. versatus* (Robertson)	B	—
2F	*Dialictus* sp. 1	G, B	—
1F	*Halictus* (*Seladonia*) *confusus* Smith	B	—
5F	*Lasioglossum* sp. nr. *coriaceum* (Smith)	2 P, B	—
1F	*Lasioglossum* (*Evylaeus*) sp. 1	—	G
1F	*Sphecodes confertus* Say	G	—
Andrenidae			
15F	*Andrena* sp. nr. *confederata* Viereck	10 P, G, B	2, G
6M	*Andrena lamelliterga* Ribble	G, B	G, B
11F	*Andrena* sp. nr. *lata* Viereck	5 P, G, B	—
1F	*Andrena melanochroa* (Cockerell)	—	G
1M	*Andrena perplexa vibernella* Graenicher	B	—
2F	*Andrena perplexa vibernella* Graenicher	2 P, G	—
5F	*Andrena rugosa* Robertson	2 P, B	—
5F	*Andrena vicina* Smith	5 P, G, B	—
1M	*Andrena* (*Micrandrena*) sp.	—	G
2F	*Andrena* sp. 1	1 P, B	—
1F	*Andrena* sp. 2	—	B
5F	*Andrena* sp. 3	3 P, B, G	G
6F	*Andrena* sp. 4	3 P, B, G	G
2F	*Andrena* sp. 5	2 P, B	—
2F	*Andrena* sp. 6	1 P, B	—
1F	*Andrena* sp. 7	—	G
1F	*Andrena* sp. 8	B	—
3F	*Andrena* sp. 9	1 P, G, B	—
1F	*Andrena* sp. 10	G	—
1M	*Andrena* sp. 11	G	—
2M	*Andrena* sp. 12	—	G
5M	*Andrena* sp. 13	G	G, B
1M	*Andrena* sp. 14	G	—
1M	*Andrena* sp. 15	B	—
3M	*Andrena* sp. 16	—	G, B
1M	*Andrena* sp. 17	—	G

Table 1. Continued.

Bee species or genus, sex and number of individuals		On Male Trees	On Female Trees
Colletidae			
8 + F	*Colletes thoracicus* Smith	6 P, G, B	—
3 + M	*Colletes thoracicus* Smith	G, B	—
1F	*Colletes willistoni* Robertson	P, B	—
1F	*Hylaeus modestus* Say	B	—
3M	*Hylaeus modestus* Say	—	G

(Fig. 3). Flowering ended on June 9; the last trees to bloom being those growing in understory areas that were shaded by taller trees.

During warm, sunny weather, individual pistillate flowers began flowering (secreting nectar) and ceased flowering (stopped nectar secretion, with their styles curled, shriveled, and brownish) within 24 hours. For example, some pistillate flowers on one tree began secreting nectar and attracted insects at noon on May 23. They had presumably been fertilized by noon the next day, because they had ceased nectar production, and no longer were attracting insects. Other pistillate flowers on the same tree bloomed on other days, so that the total flowering period of this female tree lasted 10 days. The flowering period of individual staminate flowers lasted several days. During this time, nectar droplets were continuously secreted, and the numerous anthers on each flower dehisced sequentially (Fig. 1). Staminate trees collectively and individually had a long flowering period. At mid-bloom, each tree had some branches with flowers not yet blooming, other branches with flowers in full bloom, and some branches were past bloom, with shriveled stamens falling from their flowers.

Staminate flowers had a faint, pleasant, honeylike fragrance, but pistillate flowers seemed to me to be odorless. Both pistillate and staminate flowers produced copious nectar. When first secreted, the nectar appeared as small, discrete, transparent, shiny spheres on the glabrous floral discs (Fig. 2). These later enlarged (to 0.2–0.3 mm in diameter), then (at 0.5 mm) coalesced, to cover the disc with a sheet of glistening, dense, and sweet-tasting nectar. Excess nectar may drip from the discs of pistillate flowers (Fig. 3). Once the nectar has coalesced, the floral disc beneath it loses its pale, bluish glabrous appearance, and becomes dark green. Nectar secretion by staminate flowers begins as their first anthers dehisce (Fig. 1), and ends when all anthers have shriveled and some have begun to fall off.

In order to determine whether pollination by wind and insects occurs, several branches of a pistillate tree were securely bagged prior to bloom, and the bags were left in place for a month. Brown Kraft paper bags were used to exclude both wind-borne and insect-borne pollen. Fine-mesh gauze bags were used to exclude only insects. No fruit formed on any of the hundreds of bagged flowers, even though a few of them had vestigial anthers. This showed that cross pollination by insects is required.

Several other native woody plants in the area bloomed at the same time as *N. sylvatica,* potentially competing for visits by pollinating insects. These included huckleberry, *Gaylussacia frondosa* (L.) T. and G.; American holly, *Ilex opaca* Ait.; mountain laurel, *Kalmia latifolia* L.; tuliptree, *Liriodendron tulipfera* L.; staggerbush, *Lyonia mariana* (L.) D. Don; black cherry, *Prunus serotina* Ehrh.; black locust, *Robinia pseudoacacia* L.; poison ivy, *Rhus radicans* L.; *Rubus* sp. and *Viburnum* sp. Most of these plants had conspicuous, fragrant flowers. Many of the bees that were caught on *N. sylvatica* flowers included pollen of other plants in their scopae. Allegheny chinkapin, which is very attractive to many species of bees and other insects, began to bloom a day after *N. sylvatica* finished blooming. American chestnut, *Castanea dentata* (Marsh.) Borkh., was once a dominant tree of the eastern mesophytic forest; its almost total loss must have significantly altered the numbers and diversity of insects that depended on its flowering.

Bees on *N. Sylvatica* Flowers

Bees and other insects were collected from the pistillate and staminate flowers of about 20 trees (Table 1). Binoculars were used to observe bees high in the canopy, where they could not be collected; these included numerous foraging females of *Colletes thoracicus* Smith, and both sexes of *Xylocopa virginica* (L.), including males patrolling and defending their territories. Both sexes of *C. thoracicus* were very abundant at mid-day on May 31 on a staminate tree in Greenbelt; some two females per cubic meter of canopy could be seen at a glance, while foraging for nectar and pollen. This bee is also often abundant on *Liriodendron tulipfera* and *Ilex* spp. trees. In general, more bees were seen on flowers of *N. sylvatica* that were in sunlight (in full sun or in sun flecks) than on those in shade (the shady side of the tree, or beneath taller trees, or shaded by the host's own canopy). During the course of a day, as individual *N. sylvatica* flowers became sunlit and shaded, bees usually visited them while they were in the sunshine.

Most of the bees on *N. sylvatica* flowers were short-tongued species in the genera *Andrena* and *Colletes*; over 135 individuals in 46 species, 13 genera, and 6 families were collected or seen (Table 1). Although bees predominated, other insects also visited *N. sylvatica* flowers (mostly staminate); they included thrips; syrphid, conopid, calliphorid, and other flies; *Polistes, Vespula* and solitary predaceous wasps; small parasitic wasps; carpenter ants; cantharid and cerambycid beetles; and adult sawflies.

Only two honey bees were collected or seen on flowers. They were on pistillate flowers within 50 meters of the apiary at Beltsville. At the time, this apiary had 73 large colonies with thousands of foragers in hives with 2 supers, plus 8 small colonies, or "nucs". Honey bees comprised only 3 percent of all bees collected from *N. sylvatica* flowers near the apiary at Beltsville (2 of 53), and only 1.5 percent of all bees collected (2 of 135). This result was surprising, because nectar was always abundant on pistillate and staminate flowers, and honey bees produce a large amount of honey for the commercial market from the nectar of tupelo trees (*N. aquatica*). However, *N. aquatica* and *N. sylvatica* may not be preferred hosts for honey bees. Perhaps they are forced to forage on tupelo due to the absence of other hosts in the southern swamps. Honey bees did not outcompete or displace native bees on *N. sylvatica* as expected, including trees growing near numerous hives.

The reasons for the attraction of bees and other insects to the small, green flowers of *N. sylvatica,* while more showy alternate hosts were available, were investigated. The staminate flowers have only a faint fragrance, and the radiating yellow anthers may be attractive (Fig. 1). Nectar exposed on the floral discs is readily accessible to many insects. However, if the easily ingested, noncrystallizing nectar sugars alone were the main attractant, *N. sylvatica* flowers would be expected to host a wide range of scavengers, and be teeming with these insects, as can be seen feeding on sap at slime fluxes. Instead, short-tongued bees predominated, accounting for about 70 percent of all insect visitors.

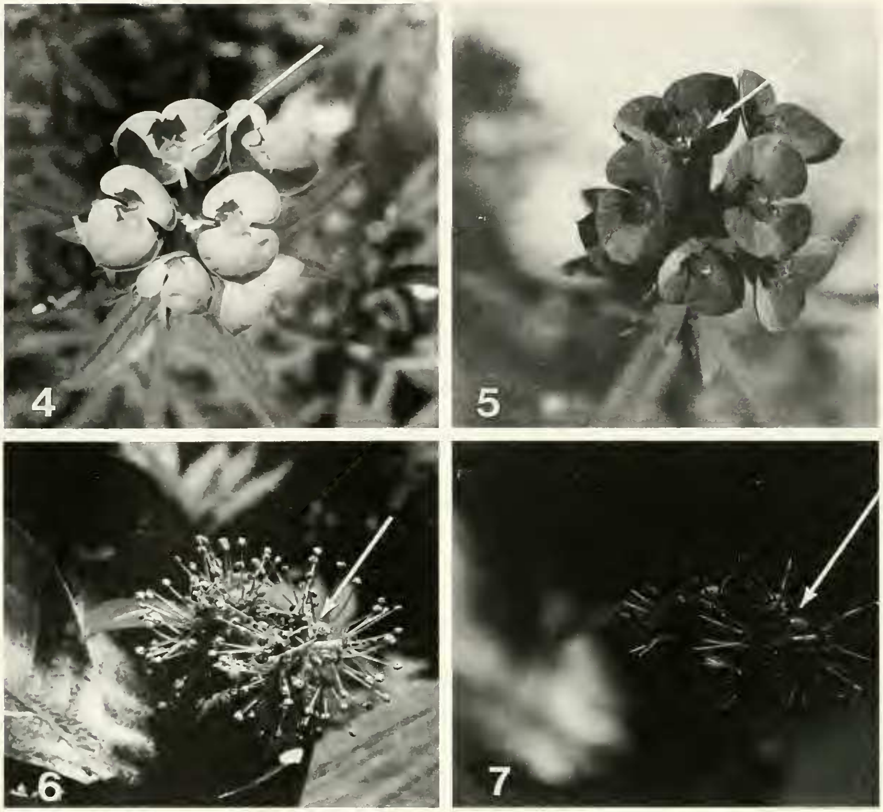
A remarkable feature of the flowers of *N. sylvatica* is the appearance of the exposed nectar when it is in sunlight. The small, spherical droplets on young flowers glitter against their background of pale blue-green, glaucous floral discs. The sheet of nectar on older flowers also glistens in the sunlight. Even slight movements of the branches cause the sunlit nectar to sparkle. The smooth, glossy upper surface of the leaves also reflects sunlight, including ultraviolet (Fig. 7). It is probable that bees may be attracted at short range to the glittering of the nectar, which substitutes for the usual showy flowers with nectar guides and distinct fragrances, found among most insect-pollinated plants. Bees and flies are attracted to small, shiny objects of metal, and to glass beads (Peisl 1997); sparkling, colorless, odorless nectar may be similarly attractive. The shiny leaves of *N. sylvatica* may also serve to attract bees to the trees, acting as if floral clusters, by assisting in their long-range orientation. Most bee-pollinated flowers have distinctive shapes and colors that are attractive to bees, including patterns that reflect or absorb ultraviolet. They enhance bees' learning and memory, thus aiding floral constancy and pollen transmission (Menzel et al. 1997, Lehrer 1997). According to Chittka et al. (1994), green leaves appear uncolored to bees (=bee-white, bee-gray, bee-black), and most flowers have contrasting hues, including the surprisingly few (4%) that reflect only in UV, which is readily seen and remembered by bees. Most flowers contrast with surrounding foliage, which tends to absorb ultraviolet. The nectar and stamens of many flowers augment nectar-guide patterns on ultraviolet-reflecting petals, by absorbing ultraviolet light; they may fluoresce (Thorp et al. 1975, Tanaka 1982). The nectar droplets and opened anthers of *N. sylvatica* also fluoresce in ultraviolet.

The flowers of cypress spurge, *Euphorbia cyparissias* (L.), are also attractive to many bees and other insects (Batra, personal observation). They resemble flowers of *N. sylvatica* in visible light, because they are mostly green to greenish-yellow, and they also have exposed droplets of nectar in shallow nectaries. This nectar glistens in direct sun. I photographed flowers of *E. cyparissias* and *N. sylvatica* in sunlight, using a filter that transmits 350–390 nm ultraviolet wavelengths (Wratten 18A filter, Nikon 55 mm f/3.5 glass lens and Tri-X film). Foliage, bracts, and other parts of both plants that had appeared green to yellowish-green in daylight absorbed ultraviolet, appearing dark. The glistening nectar strongly reflected ultraviolet, appearing white, contrasting with the plants' flowers and foliage (Figs. 4–7). Evidently, insects are attracted by the nectar's reflected ultraviolet and visible light.

Thus, like *E. cyparissias,* the nectar of *N. sylvatica* reflects ultraviolet, contrasting with surrounding UV-absorbent green foliage, pedicels, and other floral structures. The reflectance may be enhanced in young flowers by the spherical shape of the discrete droplets, which would act as convex lenses, concentrating both visible and ultraviolet light. The bluish color of the background (the glabrous surface of the disc) may enhance the attractiveness of *N. sylvatica* nectar to bees, which respond to blue colors. Floral discs of young staminate flowers that bear numerous spherical, lens-like nectar droplets (Figs. 1,2) resemble the multifaceted lenses that are used as reflectors for traffic signals.

Honeydew that is secreted by aphids on conifers attracts bumble bees from long distances (Batra 1993). It also glitters brilliantly in the sunshine, contrasting with the dark green needles of the conifers. This may be another example of attraction by nectar-reflection; something worth reflecting about. Flowers that lack showy petals and sepals or a distinct perfume, and that rely on reflectance from their exposed nectar to attract pollinators, represent a distinct category or pollination system, here termed "sparkle-flowers" (new coinage). The small, yellowish-green flowers of ivy (*Hedera helix* L.) have exposed nectar droplets borne on convex discs (Barth 1985), thus resembling *Nyssa* flowers. They attract their host-specific pollinators (*Colletes hederae* Schmidt and Westrich) only when they are in sunshine (Westrich 1996). Thus, the flowers of ivy probably are yet another example of "sparkle flowers."

In conclusion, this preliminary research demonstrates that we should not assume



Figs. 4–7. Reflecting nectar of "sparkle-flowers," as seen in sunlight and in ultraviolet (as photographed with a Wratten 18A filter, Nikon 55 mm f/3.5 glass lens and Tri-X film). Reflective nectar droplets are indicated by arrows. 4, *Euphorbia cyparissias* in sunlight. 5, The same flowers in ultraviolet; white dots are UV-reflecting nectar droplets. 6, Staminate flowers of *N. sylvatica* in sunlight. 7, The same flowers in ultraviolet; note that the glossy tops of the leaves reflect.

that honey bees (or other exotic bees) compete with, and displace, native bees, even when honey bees are abundant, and a host that is known to be visited by honey bees is being considered. It will be necessary to study the complex of bee species that visit each host species during several seasons, to allow for annual fluctuations in weather, in native and exotic bee populations, in flowering of the host, and in the presence of other simultaneously flowering host plants that may divert bees (especially wide-ranging honey bees) from the plants that are being studied. Honey bees in this study evidently had been diverted from *N. sylvatica* to other, more attractive, resources.

The variety of bees collected from *N. sylvatica* during a short time, in a small area, suggests that more extensive surveys of this and other North American trees would yield many other insects, including undescribed species. Flowering trees often produce copious amounts of nectar and pollen, yet they are relatively unexamined resources that should have profound impacts on the population dynamics of our native bees. Beekeepers are aware of the value of several species of trees as resources for honey bees.

The discovery of "sparkle-flowers," a previously unrecognized type of inflorescence, in a suburban habitat that has been investigated by many scientists, shows that new phenomena can still be revealed in such unpromising locations with the aid of simple, inexpensive equipment. The behavior of the bees as they approached flowers of *N. sylvatica* provided clues as to the attractant, much as did the behavior of insects at *Vaccinium* and *Gaylussacia* plants that had been infected by *Monilinia* fungi (Batra and Batra 1985). "Sparkle-flowers" may be a relatively common type of inflorescence, previously overlooked because they appear so inconspicuous to us.

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